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The colour white diminishes weight loss during aestivation in the arid-dwelling land snail *Sphincterochila (Albea) candidissima*

El color blanco disminuye la pérdida de peso durante la estivación en el caracol de medios áridos *Sphincterochila (Albea) candidissima*

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ABSTRACT

It has been suggested that white colour is beneficial for snails living in arid environments. In this work, shell coloration in the arid-dwelling land snail *Sphincterochila (Albea) candidissima* was manipulated during aestivation. Snails painted black lost more body weight than did control ones, presumably as a consequence of higher heat absorption. This suggests that light colour is advantageous for this land snail.

RESUMEN

Se ha sugerido que el color blanco es beneficioso para los caracoles en ambientes áridos. En el presente trabajo se manipula la coloración de la concha en el caracol de medios áridos *Sphincterochila (Albea) candidissima* durante la estivación. Los caracoles pintados de negro perdieron más peso que los caracoles que sirvieron como control, presumiblemente como una consecuencia de una mayor absorción de calor. Esto sugiere que los colores claros son ventajosos para este caracol.

KEY WORDS: *Sphincterochila candidissima*, arid environments, colouration. PALABRAS CLAVE: *Sphincterochila candidissima*, medios áridos, coloración.

INTRODUCTION

It is well established that tegument colour has important functions in camouflage, as well as in communication (e.g., BADAYEV AND HILL, 2000; THÉRY, DEBUT, GOMEZ AND CASAS, 2005; EXNEROVA, SVADORA, BARCALOVA, LANDOVA, PROKOPOVA, FUCHS AND SOCHA, 2006). The colour of teguments depends on the wavelengths that are reflected. Therefore, colouration affects the energy that is absorbed by the tegument, the amount being higher as the colour darkens. In this sense, animal colouration may also have a role in thermoregulation, especially important for arid-dwelling animals (CLOUDSLEY-THOMPSON, 1978). Terrestrial molluscs are very susceptible to dehydration (PRIOR, 1985; LUCHTEL AND DEYRUP-OLSEN, 2001), and therefore need adaptations to survive in arid envi-

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ronments. White colour may favour the success of land-snails in warm environments: White shells have a higher reflectance of sunlight (SCHMIDT-NIELSEN, TAYLOR AND SHKOLNIK, 1971), and, as a consequence, land snails with light-coloured shells register lower body temperatures (HEATH, 1975), thereby improving survival under high temperatures (RICHARDSON, 1974). This translates as a selective pressure for whiter shells in arid environments and, in fact, some studies have correlated shell colour with environment temperature (JONES, 1973; but there are exceptions: HELLER, 1984).

The snails of the genus Sphincterochila have white shells. In Sierra Elvira (SE Spain), Sphincterochila (Albea) candidissima (Draparnaud, 1801) is the most abundant gastropod (MORENO-RUEDA, 2002). Sierra Elvira has an arid environment, and sheltering in protective microhabitats may be a vital strategy against dehydration (STEINBERGER, GROSSMAN, DU-BINSKY AND SHACHAK, 1983; ARAD, GOLDENBERG AND HELLER, 1989; COOK, 2001). However, S. candidissima does not use refuges during drought periods (spring and summer) (MORENO-RUEDA, 2007; MORENO-RUEDA AND COLLANTES-MARTÍN, 2007). Because the shell of S. candidissima is pure white, I hypothesized that shell colour might contribute to the survival of S. candidissima in Sierra Elvira, explaining why this snail does not need refuges against dehydration. I investigated this hypothesis by manipulating the shell colour of S. candidissima during aestivation (painting some snails), and by examining the effect of this manipulation on the amount of body mass lost. About 80-90% of fresh body weight (shell not included) of Sphincterochila land snails is water, and, therefore, a decrease in body weight suggests a loss of water (SCHMIDT-NIELSEN ET AL., 1971; YOM-TOV, 1971; STEINBERG-ER, GROSSMAN AND DUBINSKY, 1981).

METHODS

This study was performed in Sierra Elvira (SE Spain, 37° 15′ N, 3° 40′ W), a small mountain range with a dry mesomediterranean climate (UNESCO, 1963). The study area undergoes five months of drought each year, with an average annual precipitation of 600-1000 mm (ALONSO, LÓPEZ-ALCÁNTARA, RIVAS AND IBÁÑEZ, 1985). It is, therefore, a dry zone for land snails. Table I presents climatic data during the study period, measured from the meteorological station of Pinos Puente, about three kilometres from the study area, and approximately at the same altitude (630 m. a.s.l.).

Sphincterochila candidissima is the only species of the genus Sphincterochila in Sierra Elvira (RUIZ RUIZ, CÁRCABA Pozo, CREVILLÉN PORRAS AND ARRÉBOLA BURGOS, 2006). In the study area, this species begins aestivation in April-May (MORENO-RUEDA, 2007; MORENO-RUEDA COLLANTES-AND MARTÍN, 2007). This snail adheres to rock or vegetation during aestivation. For manipulation, snails were not separated from the substrate, because this could provoke dehydration in the snails (LUCHTEL AND DEYRUP-OLSEN, 2001). For this reason, I could not measure body mass before treatment, but I collected 75 additional individuals in order to analyse the relationship between shell morphology and body mass. The experiment started on 26 June 2005. Each individual found was sequentially assigned to the control group (C), to the control of manipulation group (CM), or to the experimental group (E). Manipulation in control group was only a mark for recognition. Snails in the CM group were painted in yellow with a marker. Paint covered approximately 50% of shell surface. In the experimental group, the shell was painted black with a marker in the same way as in CM group. In total, 52 snails were used in each group (n = 156). The study area was prospected two months later (26 August 2005). Snails found were collected and measured (shell height and width) with a calliper (accuracy 0.01 mm.) and weighed with a digital balance (accuracy 0.1 g.).

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Table I. Climatic data of the meteorological station of Pinos Puente, located near of the study area, for the study period (06/26/2005 to 08/26/2005).

Tabla I. Datos climáticos de la estación meteorológica de Pinos Puente, próxima a la zona de estudio, para el período de estudio (26/06/2005 a 26/08/2005).

	Mean	S.E.	Minimum	Maximum	
Daily maximal temperature (°C)	36.8	0.36	30.7	42.9	
Daily minimal temperature (°C)	17.6	0.30	12.7	22.8	
Average daily temperature (°C)	27.0	0.27	23.4	31.3	
Daily radiation (MJ/m ²)	27.6	0.51	13.9	32.5	
Daily precipitation (mm.)	0.03	0.02	0.00	0.80	

Table II. Average weight on the day 08/26/2005, and shell height and width for the snails in the experimental (E), control (C) and control of manipulation (CM) groups. The last row shows the average weight after statistically controlling for shell height and width. The last column shows the results of ANOVA and ANCOVA. In brackets is the standard error.

Tabla II. Peso promedio el día 26/08/2005, y altura y anchura de la concha para los caracoles en el grupo experimental (E), control (C) y control de la manipulación (CM). La última fila muestra el peso promedio después de controlar estadísticamente por la altura y anchura de la concha. La última columna muestra los resultados de los tests de ANOVA y ANCOVA. Entre paréntesis el error estándar.

	E group	C group	CM group	ANOVA		
	<i>n</i> = 29	<i>n</i> = 34	<i>n</i> = 30	F	d.f.	Р
Weight (g.)	2.70 (0.09)	3.02 (0.09)	2.87 (0.09)	3.15	2, 90	< 0.05
Width (mm.)	21.49 (0.22)	21.31 (0.21)	21.33 (0.22)	0.21	2,90	0.81
Height (mm.)	16.54 (0.18)	16.77 (0.17)	16.37 (0.18)	1.33	2,90	0.27
Weight (controlled for shell size)	2.69 (0.07)	3.00 (0.06)	2.91 (0.07)	6.28	2, 88	< 0.003

The variables had a distribution similar to normal (Kolmogorov-Smirnov test, p > 0.05), and parametric statistics were used. An ANOVA was used to test the effect of the treatment on body weight, and an ANCOVA was used controlling by snail body size (height and width). For post hoc comparisons the Fisher LSD test was used. The Chisquare was used to test the probability of survival according to treatment.

RESULTS

In August, I recaptured 34 snails alive in the control group, 30 for the CM group, and 29 of the experimental group. The frequency of recaptures did not differ significantly between the three

groups (χ^2_{2} = 1.12; p= 0.57). When individuals were collected in August, there were significant differences for body mass between the treatments (Table II). Individuals of the experimental group weighed less than those in the control one (post hoc Fisher LSD, p = 0.01), while the average weight in the CM group was intermediate between the other two groups (post hoc, CM vs. C, p = 0.22; CM vs. E, p = 0.22). In the additional sample of 75 individuals, body mass was strongly predicted by shell morphology (Multiple Regression Model; $R^2 = 0.81$; $F_{2,72} = 149.0$; p < 0.001; equation: Body mass = -5.16 (SE = 0.46; $t_{72} = 11.2$) + 0.28 (SE = 0.03; $t_{72} = 10.2$) x Width + 0.14 (SE = 0.03; $t_{72} = 5.1$) x Height). There were no significant differences for body size (height and

width) between the three groups (MANOVA, Wilks = 0.94; F₄, 178 = 1.46; p = 0.22; Table II), suggesting that initial body mass did not differ among groups. When the analyses were repeated with shell height and width as a covariate, differences in weight between groups were accentuated (ANCOVA, F2, 88 = 6.28; p < 0.003; Height effect: F1, 88 = 10.90; p = 0.001; Width: F_{1,88} = 21.98; p <0.001; Table II). Differences between the control group and the experimental group increased in this analysis (post hoc, p < 0.001), while body weight in the CM group remained intermediate between the other two groups (CM vs. C, p = 0.08; CM vs. E, p = 0.08).

DISCUSSION

The findings of this experimental study show that shell colour alteration in Sphincterochila candidissima during aestivation had effects on weight loss, snails with shells painted black suffering a quicker loss of weight than control snails. The most probable mechanism behind this result is that light reflection was lower in shells painted in black, and for this reason they trapped more heat, as shown in other studies with other species of snails (e.g., HEATH, 1975). The higher the body temperature, the higher the water loss, decreasing body weight (YOM-TOV, 1971). Body size may affect the interaction between shell colour and heat absorption (SLOTOW, GOODFRIEND AND WARD, 1993), but there were no differences in body size between the groups, and differences in weight remained significant after controlling statistically for shell morphology. This weight loss presumably harms fitness, increasing the risk of mortality, especially for the smallest individuals (with less reserves), or in very dry years (RICHARDSON, 1974). Moreover, the treatment lasted only two months (although the warmest), but S. candidissima aestivates for 5-7 months in the study area (MORENO-RUEDA AND COLLANTES-MARTÍN, 2007), and therefore, the effect should be more accentuated if the entire aestivation period is considered.

The control of manipulation (CM) group, with shells painted in yellow, had weight values intermediate to the other two groups. In fact, this group is not a true control of manipulation, as colour was altered with respect to unmanipulated snails. Because their shells were darker than shells in the control group, but lighter than shells in the experimental group, the results support that weight loss is due to shell colour. As weight for the CM group was intermediate, if there was an effect of paint on weight, this cannot completely explain the differences between the control and the experimental group.

Therefore, results presented here and in the literature strongly suggest that the white colour is advantageous for survival in arid-dwelling snails. The question arises as to why white colour is not more widespread in arid environments (see, for example, HELLER, 1984). Other selective mechanisms besides thermal selection act on shell colour, such as predation (JONES, LEITH AND RAWLINGS, 1977). Lighter shells, especially those with a pure white colour as Sphincterochila candidissima, are in usually easier to detect by predators (REED AND JANZEN, 1999). However, predation on Sphincterochila candidissima is rare due to its thick shell (YANES, SUÁREZ AND MANRIQUE, 1991), and thus the absence of a strong selection by predators in this species would favour the maintenance of pure white shells.

In conclusion, this study, applying an experimental approach, supports the hypothesis that shell colour affects weight loss in arid-dwelling land-snails, and, as a consequence, fitness, by a mechanism mediated by thermoregulation.

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BIBLIOGRAPHY

- ALONSO, M. R., LÓPEZ-ALCÁNTARA, A., RIVAS, P. AND IBÁÑEZ, M., 1985. A biogeographic study of *Iberus gualtierianus* (L.) (Pulmonata: Helicidae). *Soosiana*, 13: 1-10.
- ARAD, Z., GOLDENBERG, S. AND HELLER, J., 1989. Resistance to desiccation and distribution patterns in the land snail *Sphincterochila*. *Journal of Zoology*, 218: 353-364.
- BADYAEV, A. V. AND HILL, G. E., 2000. Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. *Biological Journal of the Linnean Society*, 69: 153-172.
- CLOUDSLEY-THOMPSON, J. L., 1978. Adaptive function of the colours of desert animals. *Comparative Physiological Ecology*, 1: 109-120.
- COOK, A., 2001. Behavioural ecology: On doing the right thing, in the right place at the right time. In Barker, G. M. (Ed.): *The Biology of Terrestrial Molluscs*. CAB International. Wallingford. Pp. 447-487.
- EXNEROVA, A., SVADORA, K., BARCALOVA, S., LANDOVA, E., PROKOPOVA, M., FUCHS, R. AND SOCHA, R., 2006. Importance of colour in the reaction of passerine predators to aposematic prey: experiments with mutants of *Pyrrhocoris* apterus (Heteroptera). *Biological Journal of the Linnean Society*, 88: 143-153.
- HEATH, D. J., 1975. Colour, sunlight and internal temperatures in the land-snail *Cepaea nemoralis* (L.). *Oecologia*, 19: 29-38.
- HELLER, J., 1984. Shell colours of desert landsnails. *Malacologia*, 25: 355-359.
- JONES, J. S., 1973. Ecological genetics and natural selection in molluscs. *Science*, 182: 546-552.
- JONES, J. S., LEITH, B. H. AND RAWLINGS, P., 1977. Polymorphism in *Cepaea*: a problem with too many solutions? *Annual Review in Ecology and Systematics*, 8: 109-143.
- LUCHTEL, D. L., DEYRUP-OLSEN, I., 2001. Body wall: form and function. In Barker, G. M. (Ed.): *The Biology of Terrestrial Molluscs*. CAB International. Wallingford. Pp. 147-178.
- MORENO-RUEDA, G., 2002. Selección de hábitat por *Iberus gualtierianus, Rumina decollata* y *Sphincterochila candidissima* (Gastropoda: Pulmonata) en una sierra del sureste español. *Iberus*, 20: 55-62.
- MORENO-RUEDA, G., 2007. Refuge selection by two sympatric species of arid-dwelling land snails: Different adaptive strategies to achieve the same objective. *Journal of Arid Enviroments*, 68: 588-598.
- MORENO-RUEDA, G. AND COLLANTES-MARTÍN, E., 2007. Ciclo anual de actividad del caracol *Sphincterochila (Albea) candidissima* (Draparnaud, 1801) en un medio semiárido. *Iberus*, 25: 49-56.

- PRIOR, D. J., 1985. Water-regulatory behaviour in terrestrial gastropods. *Biological Reviews*, 60: 403-424.
- REED, W. L. AND JANZEN, F. J., 1999. Natural selection by avian predators on size and colour of a freshwater snail (*Pomacea flagellata*). Biological Journal of the Linnean Society, 67: 331-342.
- RICHARDSON, A. M. M., 1974. Differential climatic selection in natural population of land snail Cepaea nemoralis. Nature, 247: 572-573.
- RUIZ RUIZ, A., CÁRCABA POZO, A., PORRAS CRE-VILLEN, A. I. AND ARRÉBOLA, J. R., 2006. Guía de los caracoles terrestres de Andalucía. Fundación Gypaetus, Seville.
- SCHMIDT-NIELSEN, K., TAYLOR, C. R. AND SHKOLNIK, A., 1971. Desert snails: problems of heat, water and food. *Journal of Experimental Biology*, 55: 385-398.
- SLOTOW, R., GOODFRIEND, W. AND WARD, D., 1993. Shell colour polymorphism of the Negev desert landsnail, *Trochoidea seetzeni*: the importance of temperature and predation. *Journal of Arid Environments*, 24: 47-61.
- STEINBERGER, Y., GROSSMAN, S. AND DUBINSKY, Z., 1981. Some aspects of the ecology of the desert snail Sphincterochila prophetarum in relation to energy and water flow. Oecologia, 50: 103-108.
- STEINBERGER, Y., GROSSMAN, S., DUBINSKY, Z. AND SHACHAK, M., 1983. Stone microhabitats and the movement and activity of desert snails, Sphincterochila prophetarum. Malacological Review, 16: 63-70.
- THÉRY, M., DEBUT, M., GOMEZ, D. AND CASAS, J., 2005. Specific color sensitivities of prey and predator explain camouflage in different visual systems. *Behavioral Ecology*, 16:25-29.
- UNESCO, 1963. Recherches sur la zone aride. Etude écologique de la zone méditerraéenne. Carte bioclimatique de la zone méditerranéenne. Notice explicative. UNESCO. Paris.
- YANES, M., SUÁREZ, F. AND MANRIQUE, J., 1991. La cogujada montesina, *Galerida theklae*, como depredador del caracol *Otala lactea*: comportamiento alimenticio y selección de presa. *Ardeola*, 38: 297-303.
- YOM-TOV, Y., 1971. Annual fluctuations in the water content of desert snails. *Malacological Review*, 4: 121-126.